

# Brood cells like conifer cones: the peculiar nesting biology of the osmiine bee *Hoplitis (Alcidamea) curvipes* (Morawitz, 1871) (Hymenoptera, Megachilidae)

Sergey P. Ivanov<sup>1</sup>, Alexander V. Fateryga<sup>2</sup>, Andreas Müller<sup>3</sup>

**1** Institute of Biochemical Technology, Ecology and Pharmacy of the V.I. Vernadsky Crimean Federal University, Vernadskogo Ave. 4, 295007 Simferopol, Russia **2** .I. Vjazemsky Karadag Scientific Station – Nature Reserve of RAS – Branch of A.O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Nauki Str. 24, Kurortnoye, 298188 Feodosiya, Russia **3** ETH Zurich, Institute of Agricultural Sciences, Biocommunication and Entomology, Schmelzbergstrasse 9/LFO, 8092 Zurich, Switzerland

Corresponding author: Alexander V. Fateryga ([fater\\_84@list.ru](mailto:fater_84@list.ru))

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## Abstract

Two nests of *Hoplitis curvipes* are described from Apulia (Italy) and Dagestan (Russia). Both nests consisted of two brood cells placed side by side under a stone. The cells were neither attached to each other nor to the substrate. They were constructed from leaf fragments, which were imbricately arranged, forming a cone-like structure; each leaf fragment consisted of a basal part that was masticated to leaf pulp and an apical part that protruded freely from the cell wall. The cell wall was formed by the fusion of the masticated basal parts of the leaf fragments and thus entirely consisted of leaf pulp. The cell was sealed with a closing plug made of pure leaf pulp; a few leaf fragments were glued to its outer surface. The cocoon consisted of two layers: the outer layer was restricted to the anterior portion of the cell and had several longitudinal air-exchange slits on its lateral surface, while the inner layer had an air-exchange orifice in its most anterior dome-shaped top. Results of measurements of brood cell dimensions and contents are provided. The nesting biology of species of the *H. curvipes* group is discussed.

## Keywords

Anthophila, Apiformes, bionomics, Caucasus, Gargano, *Hoplitis mitis*, megachilid bees, Palaearctic region



## Introduction

The genus *Hoplitis* Klug, 1807 is distributed in the Palaearctic, the Nearctic, and the Afrotropical region; a few species also occur in the Oriental region (Michener 2007). It is the largest genus of the osmiine bees (Hymenoptera, Megachilidae, Osmiini) with 389 species described so far (Müller 2023). The genus is especially diverse in the Palaearctic region, where 14 subgenera and 313 species occur (Praz et al. 2008; Ungricht et al. 2008; Sedivy et al. 2012; Müller 2023). The nesting biology of *Hoplitis* is extremely diverse and encompasses the whole diversity observed in the osmiine bees (Müller 2023). The 110 species, for which nests have been found so far, build their brood cells in self-excavated burrows in the ground or pithy stems, in various kinds of pre-existing cavities (such as hollow stems, insect burrows in wood or pithy stems, abandoned nests of other bees and wasps, rock and stone crevices, rarely galls or empty snail shells), or construct them freely on the surface of rocks or stones, usually in depressions; a few species are kleptoparasitic. Many species of *Hoplitis* build brood cells with complete constructed lateral walls. Other species only divide the nest cavity into cells with transverse partitions and seal it with a closing plug at or near its opening. The building material used for nest and cell construction is also very diverse; depending on the subgenus or species, mud and pebbles, leaf pulp, leaf fragments, petals or pith are used alone or in diverse combinations (Michener 2007; Sedivy et al. 2012; Müller 2023).

*Alcidamea* Cresson, 1864 is one of the largest subgenera of *Hoplitis*. It occurs in the Palaearctic and the Nearctic region; there are 81 described species, 64 of which occur in the Palaearctic (Michener 2007; Ungricht et al. 2008; Müller 2023). Most representatives of this subgenus nest above ground, mostly in self-excavated burrows in pithy stems or in pre-existing cavities. They usually use plant material for nest and cell construction, particularly leaf pulp, which is sometimes mixed with pith or sand (Müller 2023). One Nearctic species, *Hoplitis biscutellae* (Cockerell, 1897), is known to collect resin (Rust 1980). The Palaearctic species *Hoplitis tuberculata* (Nylander, 1848) uses significant amounts of small pebbles and soil particles, which are densely packed between partitions made of leaf pulp (Müller 2015). Bees of the subgenus *Alcidamea* usually do not construct lateral cell walls except for some species of the *Hoplitis fulva* group, which make complete cells of plant pulp in either self-excavated or pre-existing cavities in the ground (Marikovskaja 1968; Ivanov and Fateryga 2018).

The most unusual nesting habits are, however, known for *Alcidamea* species of the *Hoplitis curvipes* group, which contains five species. Nests of one of them, *Hoplitis mitis* (Nylander, 1852), have been described so far. This species nests below stones, in rock crevices, in grass tussocks, between dried leaves or in old cells of other bees. The brood cells, which are built singly or in small groups of up to 12, entirely consist of leaf fragments imbricately glued together, forming a cone-like structure. The cell closure is made of leaf pulp, which is occasionally reinforced by sand grains or leaf fragments (Maneval 1925; Koller and Hamann 1950; Bonelli 1967; Müller et al. 1997; Westrich 1989). Trophic relationships are known for four species of the *H. curvipes* group: *H. mitis* is oligolectic on Campanulaceae, particularly *Campanula* L. (Fig. 6G), *H. curvipes* (Morawitz, 1871) is oligolectic on *Allium* L. (Amaryllidaceae) (Fig. 1E), *H. tricolor* (Saunders, 1908) is probably oligolectic on *Reseda* Tourn. ex L. (Resedaceae), and *H. epeoliformis* (Ducke, 1899) is polylectic (Müller 2023).



*Hoplitis curvipes* is known from Spain, France, Italy (including Sicily), Greece, Bulgaria, Russia (Dagestan), Azerbaijan, Turkey, and Syria (Müller 2023). In spite of its relatively large distribution area, nests of *H. curvipes* have not been described so far. The purpose of the present contribution is to report the nesting biology of this rare species based on two nests found in Italy and Russia.

## Material and methods

Field observations were carried out in Apulia (Italy) in the vicinity of San Giovanni Rotondo (Monte Gargano, Province of Foggia, 41°42'44"N, 15°44'11"E, ca. 600 m a.s.l.) on 5 July 1994 and in Dagestan (Russia) in the vicinity of Talgi (foothills of the Greater Caucasus, Makhachkala urban okrug, 42°52'36"N, 47°26'42"E, ca. 270 m a.s.l., Fig. 1A) on 13 and 27 June 2021.

The nest from Dagestan was first recorded on 13 June when it was provisioned by the female bee. During the second visit on 27 June, the nest was completed and consisted of two brood cells, which were transported to the laboratory, where they were kept in outdoor conditions in the shade. In January 2022, the two cells were separated from each other, softened in a humid environment, and dismantled. Leaf fragments were detached from the cell walls, pressed between sheets of paper, and dried. They were measured with an ocular micrometer scale of an MBS-9 stereomicroscope and weighed with a precise torsion balance. The cells with the outer coverage of leaf fragments removed were subjected to longitudinal dissection. The cocoons with fecal pellets were removed from the cells. The thickness and dimensions of cell walls and cocoons were measured. The cell walls, the cocoons with fecal pellets, and the prepupae found inside the cocoons were weighed. The prepupae were placed into glass tubes sealed with cotton plugs and kept under outdoor conditions. An emerged bee specimen was deposited in the collection of the V.I. Vernadsky Crimean Federal University.

To ascertain how much of the initial leaf fragments was masticated to leaf pulp, the following calculation was performed. We supposed that the initial average length of the leaf fragments of a brood cell consisted of the sum of the average length of the basal parts of the fragments, which had been masticated to leaf pulp ( $l_1$ ), and the average length of the intact ends of the fragments ( $l_2$ ). The total mass of the building material consisted of the mass of the cell wall consisting of leaf pulp ( $m_1$ ) and the total mass of the removed intact ends of the leaf fragments ( $m_2$ ). If all leaf fragments would be parallel-sided,  $l_1$  could be calculated as  $m_1$  multiplied by  $l_2$  and divided by  $m_2$ . However, the leaf fragments were approximately 1.5 times broader at their base than at their apex due to apical narrowing. Therefore, the average length of the masticated basal part of a leaf fragment was calculated according to the following formula:

$$l_1 = \frac{m_1 \times l_2}{1.5m_2}.$$



Photographs of the nest were taken with a Canon EOS RP and a Canon EOS Rebel T2i digital camera, a Sigma AF 105 mm f/2.8 and a Tamron SP AF 90 mm f/2.8 Di macro lens, and a Yongnuo YN-14EX macro flash.

Nest architecture and brood cell structure of *Hoplitis curvipes* were compared with those of *H. mitis* based on literature data (Maneval 1925; Koller and Hamann 1950; Bonelli 1967; Westrich 1989) and four nests discovered in the Swiss and Italian Alps (Zeneggen/Valais, 15 July 1990; Val Piora/Ticino, 30 July 1991; St. Pierre/Aosta Valley, 8 July 1996; Surses/Grisons, 10 July 2021).

## Results

### Nesting sites and nest architecture

The nesting site of *Hoplitis curvipes* in the Monte Gargano/Apulia was situated on an extensively used stony pasture. The nest was found on the ground under a stone. It consisted of two brood cells, which had been built side by side but did not adhere to each other. The cells were constructed from leaf fragments, which were imbricately glued together, forming a cone-like structure (Fig. 1F).

The nesting site in Dagestan was situated on an abandoned open mine covered with sparse herbaceous vegetation with solitary shrubs. No flower-visiting individuals of *H. curvipes* were observed. However, four males of this species were recorded in inflorescences of *A. rotundum* L. s. l. (= *A. erubescens* sensu Grossh., non K. Koch), where they slept during a thunderstorm (Fig. 1E). This plant taxon may represent a separate undescribed species but additional data are required to confirm this assumption (Seregin 2004).

The nest was found due to the observation of the female bee, which was periodically entering the underside of a medium-sized stone (Fig. 1B). After removing this stone two weeks later, the completed nest was found located between several much smaller stones (Fig. 1C). Similar to the nest from Apulia, this nest also consisted of two sub-vertical brood cells, which had been built side by side. The cell, which had been made by the female bee first (hereafter, cell No. 1), was situated lower than the subsequently constructed cell (hereafter, cell No. 2), so that the closing plug of cell No. 1 was approximately at the same level as the medial part of cell No. 2 (Figs 1D, 2A). The cells were neither attached to each other nor to the surrounding stones and could therefore be easily removed. In external view, they consisted of leaf fragments, which were imbricately glued together, forming a cone-like structure like the nest from Apulia.

### Brood cell structure

The examination of the nest from Dagestan revealed that the outer coverage of leaf fragments concealed the cell wall made of leaf pulp (Fig. 2C, D). However, the cell wall was not first made by the bee from leaf pulp and then covered with leaf fragments. Instead, each leaf fragment was added to the growing cell wall with its basal part, which

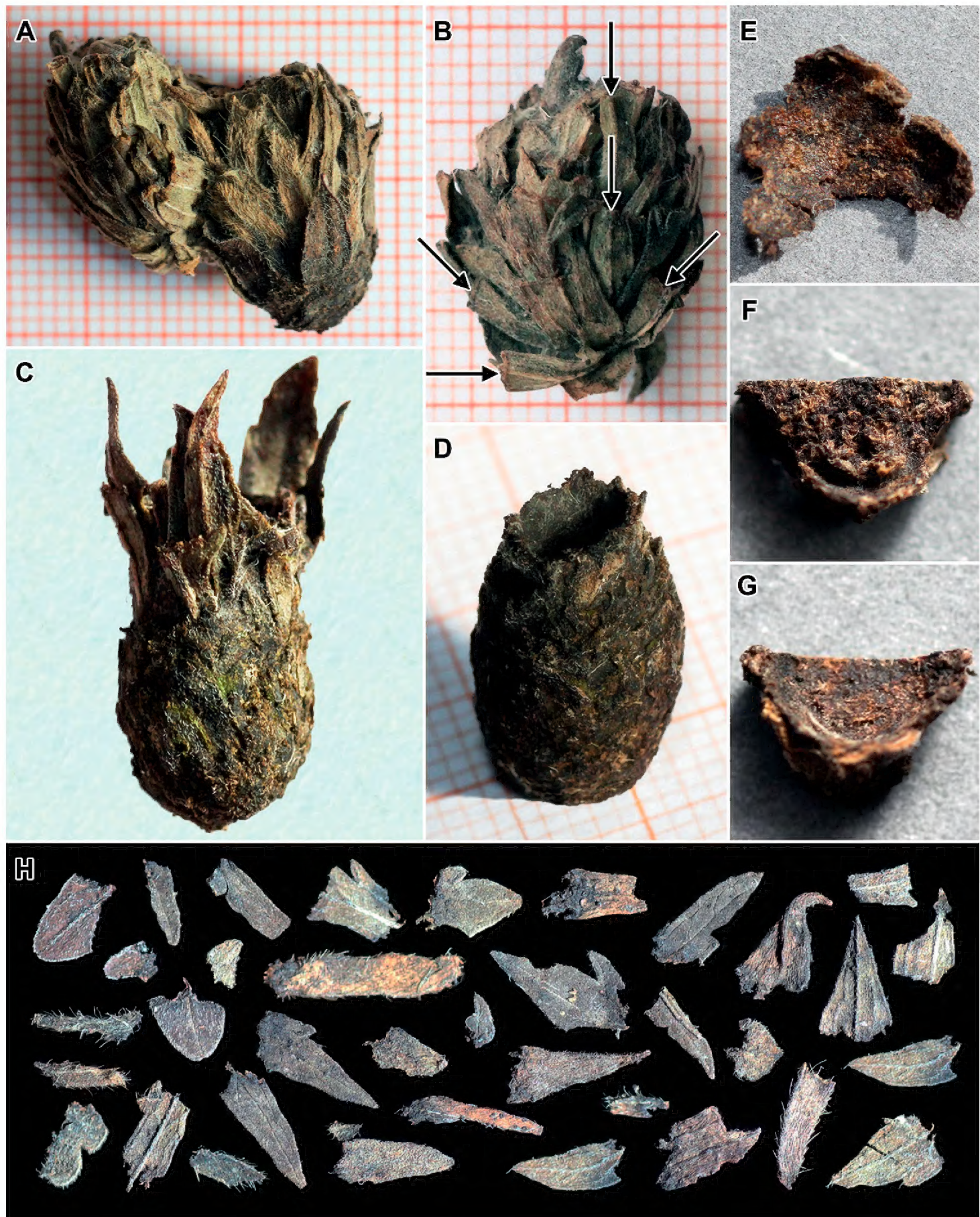




**Figure 1.** Bionomics of *Hoplitis curvipes* **A** habitat in Dagestan **B** medium-sized stone, under which a female bee entered (arrow) **C** position of the nest under the stone after its removal **D** extracted nest consisting of two brood cells **E** male sleeping in an inflorescence of *Allium rotundum* s. l. **F** nest from Apulia after removal of covering stone consisting of two brood cells with the female entering a cell. Scale bar: 1 cm (**D**).

had been masticated to leaf pulp. Thus, each intact leaf fragment projecting from the cell wall was a shortened remainder of a longer initial leaf fragment, which had been processed to leaf pulp at its base. Therefore, the outer surface of the cell wall was rough





**Figure 2.** Nest structure of *Hoplitis curvipes* **A** overview of the two-celled nest from Dagestan **B** cell No. 2 (arrows indicate leaf fragments cut from leaves from which other fragments had been previously cut as indicated by their cut apexes) **C** cell after removal of most leaf fragments **D** cell after removal of all leaf fragments **E** part of cell wall from inside **F** part of cell plug from inside **G** part of cell plug from outside **H** intact apical parts of leaf fragments removed from the cell wall.

due to the remnants of the removed intact apical parts of leaf fragments. In contrast, the inner surface of the cell wall was rather smooth (Fig. 2E). The cell was sealed with a closing plug made of pure leaf pulp; its inner surface was irregularly rough (Fig. 2F),



whereas the outer surface was evenly concave and rather smooth (Fig. 2D, G). In both cells, a few leaf fragments were glued to the outer surface of the plug (Fig. 1D).

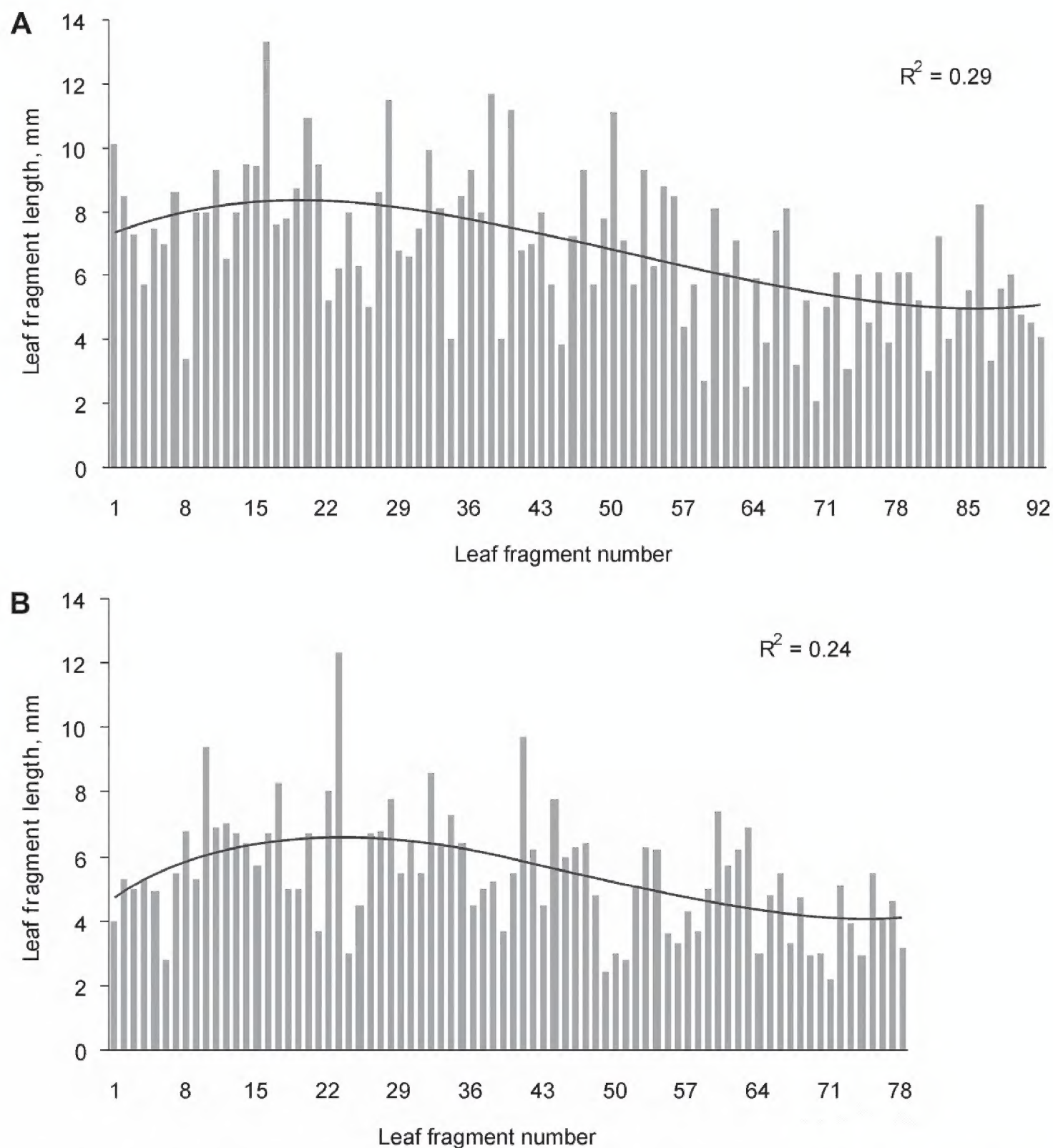
Cell No. 1 was larger and made from a higher number of leaf fragments than cell No. 2 (Table 1). Both the total mass of the intact apical parts of the leaf fragments and the total mass of the building material comprising both the masticated basal and the intact apical leaf fragment parts were also larger in cell No. 1. However, the total mass of leaf pulp originating from the masticated basal parts was larger in cell No. 2, as was the thickness of the cell wall. Therefore, the leaf fragments used by the female bee were probably masticated at their base to a higher percentage in cell No. 2. This is in line with the finding that the average length of the intact apical parts was larger in cell No. 1, whereas the calculated average length of the initial leaf fragment length was nearly equal (about 9 mm) in both cells (Table 1).

**Table 1.** Dimensions and contents of the two brood cells of a single nest of *Hoplitis curvipes* from Dagestan.

Parameter	Cell No. 1 (male progeny?)	Cell No. 2 (female progeny)
Cell outer length (without coverage of leaf fragments), mm	13.8	11.6
Cell outer width (without coverage of leaf fragments), mm	10.2	8.8
Cell wall thickness in medial part (without coverage of leaf fragments), mm	0.24	0.29
Total mass of leaf pulp from cell walls and plug, mg	78	100
Number of leaf fragments used for cell walls and plug	92	78
Average length of the intact apical part of the leaf fragments (mean $\pm$ confidence interval, $p = 0.05$ ), mm	$6.79 \pm 0.47$	$5.43 \pm 0.41$
Total mass of the intact apical parts of the leaf fragments, mg	161	100
Estimated average length of the basal part of the leaf fragments, which have been masticated to leaf pulp, mm	2.19	3.62
Estimated average length of the initial leaf fragments, mm	8.98	9.05
Total mass of the building material, mg	239	200
Cocoon outer length, mm	12.9	10.7
Cocoon outer width, mm	8.6	7.2
Cocoon wall thickness (inner layer) in medial part, mm	0.1	0.1
Cocoon mass (with fecal pellets), mg	83	76
Prepupa mass, mg	136	97
Total cell mass (with all contents), mg	458	373

The intact apical parts of the leaf fragments removed from the cell wall had variable lengths ranging from 2.1 to 13.3 mm. They were arranged irregularly so that long fragments imbricately alternated with short ones. However, a general trend was found for both cells, when all intact apical fragments were measured in the order of their application to the cell wall by the female bee: on average, the longest fragments were present in the second quarter, while the shortest fragments were found mainly in the fourth (anterior-most) quarter (Fig. 3). Probably, the female bee cut approximately equally long fragments from the plant source, but then masticated their basal ends to various degrees, so that a longer or shorter apical part remained. If a larger part remained, a smaller amount of leaf pulp was integrated into the growing cell wall, and vice versa. This is consistent with the thickness of the cell wall, which was thinnest in its medial part, where the longest intact leaf fragments were found on average (Fig. 4A).

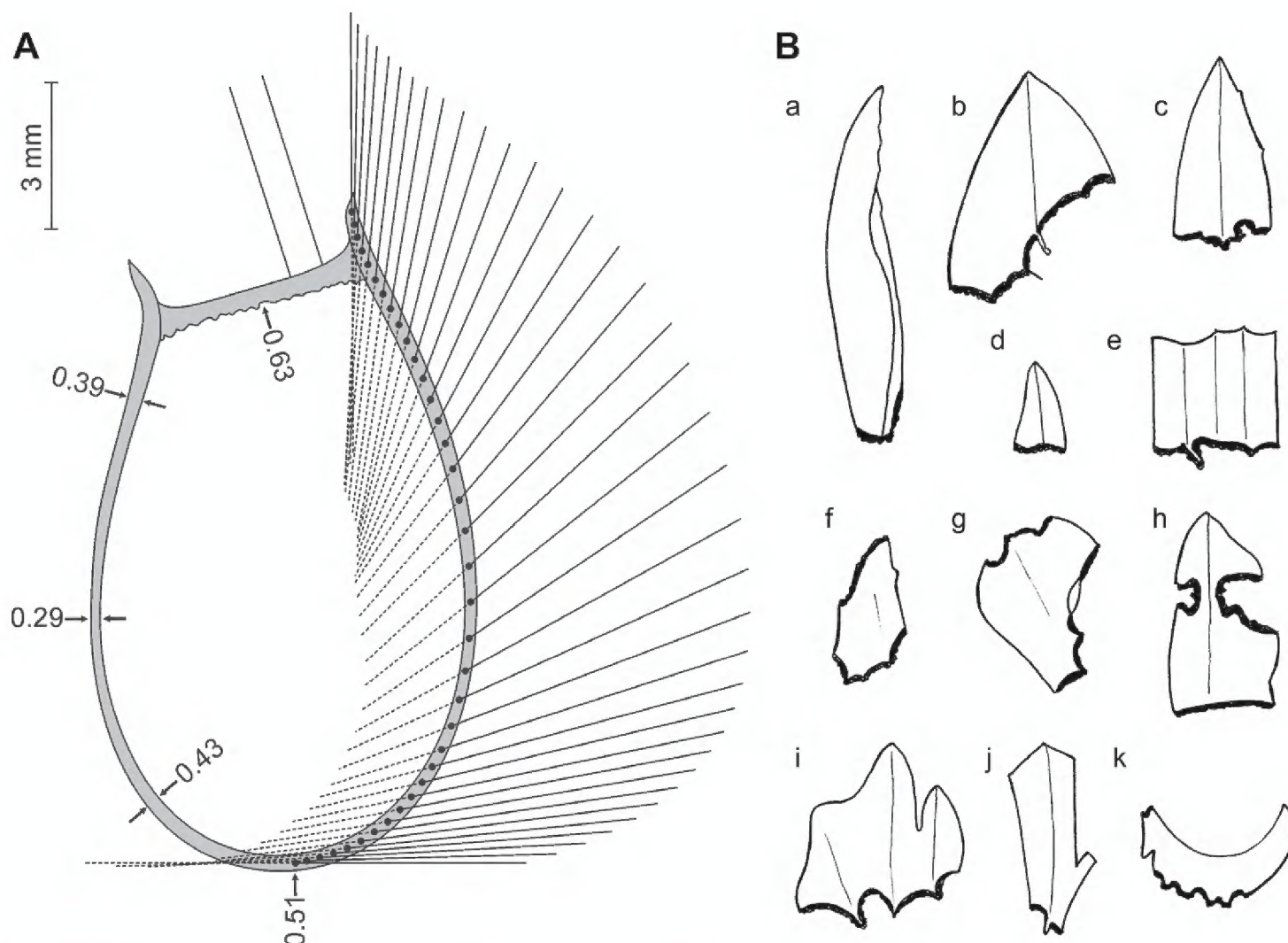




**Figure 3.** Length of the intact apical parts of the leaf fragments from two cells of *Hoplitis curvipes* from Dagestan, with cubic polynomial approximations **A** cell No. 1 **B** cell No. 2.

The shape of the intact part of the leaf fragments varied (Figs 2H, 4B). It depended mostly on the plant species from which they had been cut. At least five plant species were used by the female bee as the source of the leaf fragments. About 77% of the fragments belonged to an unidentified species with acutely narrowed apex and short trichomes on the underside. About 17% of the fragments were of another unidentified species with a similar leaf shape but with longer trichomes on both upper side and underside. About 4% of the fragments had a rounded apex and also remained unidentified, whereas about 2% of the fragments were of a species of grass (Poaceae) and at least one fragment with a crenated lateral margin originated from *Teucrium* sp. (Lamiaceae).





**Figure 4.** Nest structure of *Hoplitis curvipes* **A** scheme of cell No. 2 of the nest from Dagestan showing the thickness of cell wall and closing plug on the left and the orientation of the leaf fragments incorporated into the cell wall on the right (solid lines correspond to the length of the intact apical parts of the leaf fragments according to the approximation in Fig. 3B, dotted lines represent supposed length of the basal parts of the leaf fragments being masticated to leaf pulp) **B** various examples of intact apical parts of leaf fragments removed from the cell wall.

The base of each intact apical leaf fragment had a chewed margin (Fig. 4B), indicating that the part behind it had been masticated to leaf pulp and incorporated into the growing cell wall. This margin was sometimes straight (Fig. 4B: d, h), but often of irregular shape (Fig. 4B: b, c, i). The irregular margin might be explained by the assumption that the female bee chewed soft parts of the leaf blade but left veins intact. Some leaf fragments had chewed margins not only along the base but also at the apex (Fig. 4B: f, g) or on the lateral sides (Fig. 4B: h). This suggests that the female bee masticated these parts of the leaf fragment only after its base had been incorporated into the cell wall and that she used the resulting leaf pulp to reinforce the cell walls from inside.

The apical margin of some leaf fragments was cut. These fragments were evidently cut from leaves, from which another fragment had been previously cut (Figs 2B, 4B: e, j, k), and suggest that the female bees prefer to collect the nest building material at the very same place. This assumption is supported by the fact that cell No. 2 had more leaf fragments with cut apical margins (20 fragments, 25.6%) than cell No. 1 (six fragments, 6.5%), suggesting that the female bee found a rewarding leaf source during the



construction of cell No. 2. Generally, the shape of the leaf fragments did not seem to be important for the female bee, since even longitudinally folded leaves were applied to the cell walls without unfolding them (Fig. 4B: a).

### Cocoon structure and development of prepupae

The cocoon of *Hoplitis curvipes* filled the entire inner surface of the brood cell, neatly corresponding to the cell shape (Fig. 5F–H). It consisted of two layers. The walls of both layers were rather thick, presumably airtight, and largely consisting of a solid brown matrix, which was matt on its outside (Fig. 5A). The outer layer (Fig. 5D: b) covered the inner surface of the closing plug and the most anterior part of the lateral cell walls. This layer had several longitudinal slits on its lateral surface (Fig. 5A), which probably served as air-exchange portals. Below the slits, the outer layer was fused to the inner layer. The inner layer was rather shining on its inside, especially in its posterior half (Fig. 5B, C, H), whereas the anterior half was less shining due to its coverage with free silk strands, which were not incorporated into the matrix (Fig. 5D: e). In its most anterior part, the inner layer had a dome-shaped summit separated from the outer layer by a narrow space. The walls of this “dome” (Fig. 5D: f) gradually became thinner towards the summit, where a small orifice served as air-portal (Fig. 5D: d). The narrow space between the outer and the inner cocoon layer (Fig. 5D: c) was filled with concentric air-permeable “films” woven from silk strands. These “films” covered also the inner side of the air-exchange slits of the outer cocoon layer. The fecal pellets lay densely packed outside the cocoon on its anterior top (Fig. 5E).

Cell No. 1 contained a larger cocoon and a larger prepupa than cell No. 2 (Table 1). The prepupa from cell No. 2 pupated in 2022 and a female bee emerged from it, while the prepupa from cell No. 1 remained hibernating for a second winter. It is known since the original description by Morawitz (1871) that males of *H. curvipes* are larger than females, suggesting that the prepupa from cell No. 1 was a male. Unfortunately, this prepupa died in May 2023 rendering sex determination impossible.

### Comparison with *Hoplitis mitis*

The examination of four nests of *Hoplitis mitis* revealed close similarities, but also some differences compared to *H. curvipes*. The structure of the cells, which were 10–12 mm long and 8–9 mm wide, proved to be largely identical as revealed by the following characteristics: i) the cells of *H. mitis* were constructed from imbricately arranged leaf fragments, which formed a cone-like structure (Fig. 6A, B, D, E, F); ii) the leaf fragments consisted of a basal part that was chewed to leaf pulp and an apical part that protruded from the cell; the cell wall was formed by the fusion of the masticated basal parts of the leaf fragments and thus had a smooth inner surface (Fig. 6C); iii) the cells were sealed with a 1 mm thick plug made of leaf pulp, into which a few pieces of leaf





**Figure 5.** Nest contents of *Hoplitis curvipes* from Dagestan **A** cocoon from cell No. 1 from outside **B** same, from inside **C** cocoon from cell No. 2 from inside **D** anterior part of cocoon in longitudinal section (**a** = cell wall **b** = outer cocoon layer **c** = cavity filled with concentric “films” woven from silk strands **d** = air portal opening **e** = silk strands below the air portal **f** = inner cocoon layer) **E** anterior top of cocoon from above showing amassed fecal pellets **F** dissected cell No. 1 with prepupa hibernating in cocoon **G** same, cell No. 2 **H** dissected cell No. 1 with cocoon after removal of prepupa.

fragments were incorporated by their chewed base; these fragments were directed in longitudinal direction to the cell and slightly curved inwards, so that the nest plug was no longer visible (Fig. 6B, D).





**Figure 6.** Bionomics of *Hoplitis mitis* **A** nest in dorsal view consisting of three brood cells, which were hidden among dead blades in a grass tussock (Surses, Grisons, Switzerland) **B** same nest as above in frontal view with one brood cell still being provisioned **C** inner surface of brood cell **D** nest consisting of three brood cells, which were hidden under a removed stone (Zeneggen, Valais, Switzerland) **E** single brood cell, which was hidden in dense plant litter (Val Piora, Ticino, Switzerland) **F** single brood cell attached to a stem (St. Pierre, Aosta Valley, Italy) **G** female collecting pollen on *Campanula rotundifolia* (Bräntschi, Valais, Switzerland).

In contrast, some nests of *H. mitis* differed from those of *H. curvipes* in the following characteristics: iv) the brood cells of *H. mitis* may adhere to each other (Fig. 6A, B, D) by smoothed-out leaf pulp from chewed leaf margins, whereas the brood cells



in both discovered nests of *H. curvipes* lay freely side by side; v) while in most nests of *H. mitis* the brood cells did not adhere to the substrate as in *H. curvipes*, one brood cell of *H. mitis* was found attached to a plant stem (Fig. 6F); interestingly, in this cell the leaf fragments were more irregularly arranged and not all aligned longitudinally to the cell axis as is the case for the free-lying cells (Fig. 6A, B, D, E); this more irregular arrangement of the leaf fragments was probably due to the necessity to build part of the cell from the side rather than evenly from the posterior to the anterior end.

Our examination of the four nests of *H. mitis* confirmed the findings of other authors (Westrich 1989 and references therein) except for characteristic ii), which is described here for the first time.

## Discussion

In the present study, nest architecture and brood cell structure of *Hoplitis curvipes* are described for the first time. The nesting biology of *H. curvipes* is very similar to that of *H. mitis*, which also belongs to the *H. curvipes* species group of the subgenus *Alcidamea* and whose nesting biology has been described by several authors (Maneval 1925; Koller and Hamann 1950; Bonelli 1967; Müller et al. 1997; Westrich 1989). Both species construct the brood cells from leaf fragments, which are imbricately glued together resulting in a cone-like structure of the cell.

Both nests of *H. curvipes* discovered at two localities 2500 km apart were largely identical: they consisted of two brood cells, which lay freely side by side under a stone and adhered neither to each other nor to the surrounding substrate. Whether these characteristics are universal for *H. curvipes* across the species' entire distribution range is unclear due to the small number of nests discovered so far. It may be possible that the species is more flexible with respect to nesting site or nest architecture as is the case for *H. mitis*, which shows an amazing variability in its nesting behaviour (Maneval 1925; Koller and Hamann 1950; Bonelli 1967; Müller et al. 1997; Westrich 1989; present study): i) *H. mitis* constructs its brood cells either in pre-existing cavities (below stones, rock crevices, abandoned cells of other bees), in vegetation (grass tussocks, plant litter) or attached to plant stems or in angles of pine crotches; ii) the nests contain a varying number of brood cells ranging from 1 to 12, which lie freely side by side or are (partly) attached to each other; iii) the leaf fragments for cell construction are collected on various plant taxa; and iv) the cell closure made from leaf pulp is occasionally reinforced by sand grains.

The nests of *H. curvipes* and *H. mitis* are not only unique among species of the subgenus *Alcidamea*, but also among all other osmiine bees. As reviewed in the Introduction, most other *Alcidamea* species nest in self-excavated or pre-existing cavities and use leaf pulp as building material. Representatives of other taxa of osmiine bees build their nests also from materials other than leaf pulp, such as mud and pebbles or petals. Whole petals or large petal pieces are used by *Hoplitis* species of the subgenus *Anthocopa* Lepeletier & Serville, 1825 and *Osmia* species of the subgenus *Tergosmia* Warncke, 1988 (Rozen et al. 2010; Müller 2020). Although petals are quite similar to leaf fragments, they are applied in a different way for cell construction by *Anthocopa*



and *Tergosmia* species than the leaf fragments in *H. curvipes* and *H. mitis*. Species of *Anthocopa* use the petals to merely line the walls of brood cell cavities and nest burrows, while species of *Tergosmia* construct three-layered cells consisting of two layers of petals that sandwich a thin middle layer of mud (Ivanov and Filatov 2008; Rozen et al. 2010; Müller 2020). The unusual structure of the brood cells of species of the *H. curvipes* group, which do not require the support of the surrounding substrate, enables the construction of nests in cavities of various sizes. One nest of *H. mitis* consisting of six loosely attached cells was even found in the angle of the lowest crotch of a 0.8 m tall pine tree (Koller and Hamann 1950).

Most probably, the ancestors of the *H. curvipes* species group constructed their brood cells from leaf pulp alone, but then evolved to leave the apical parts of the collected leaves unmasticated. This is consistent with the reconstructed phylogeny of the genus *Hoplitis*, which placed *H. curvipes* and *H. mitis* as members of the same clade amidst and not basal to species of *Alcidamea*, which use leaf pulp as nest building material (Sedivy et al. 2012). Within the family Megachilidae, the use of leaf fragments for brood cell construction is most typical for numerous species of the genus *Megachile* Latreille, 1802 (Megachilini), which, however, differ from *H. curvipes* and *H. mitis* by their habit to usually cut regularly circular to elliptical leaf pieces (Michener 2007; Ivanov and Zhidkov 2010; Gonzalez et al. 2019). Some *Megachile* species, however, masticate the margins of the cut leaf pieces in order to glue them together (Ivanov and Filatov 2008). As in the *H. curvipes* species group, the leaf-cutting behaviour of *Megachile* probably evolved from ancestors, which used leaf pulp as the main nest building material, but did not completely masticate the cut leaves (Michener 2007; Gonzalez et al. 2019).

Interestingly, the brood cells of species of the *H. curvipes* group are most similar to those of communal wasps of the Indo-Malayan genus *Calligaster* de Saussure, 1852 (Hymenoptera, Vespidae, Zethinae). These wasps construct aerial nests with several brood cells attached together side by side; the cells are cone-shaped and made from leaf fragments, which are imbricately arranged (Nugroho et al. 2016). The difference of these nests from those of the *H. curvipes* species group is that the free apical ends of the leaf fragments are always directed to the posterior end of the cell rather than to the anterior one. Thus, the nests of these wasps look like “inverted” cones, which is an interesting example of convergent evolution of a similar cell structure in solitary bees and vespid wasps.

The cocoon of *H. curvipes* has a structure which corresponds to the generalized scheme of the osmiine bee cocoon with an outer and an inner layer (Rozen and Praz 2016). The outer layer is restricted to the anterior portion of the cell and separated from the inner layer by a narrow space. The inner layer is mostly airtight except for an air-exchange portal at the anterior top. In *H. curvipes*, additional air-exchange slits occur at the lateral sides of the outer layer. In combination, these structures provide humidity control and air exchange and simultaneously serve as a barrier against parasites and predators (Rozen and Praz 2016). A similar structure of the cocoon (“cocoon with an arch”) is found in some chrysidid wasps of the genera *Omalus* Panzer, 1801, *Pseudomalus* Ashmead, 1902, and *Chrysellampus* Semenov, 1932 (Hymenoptera, Chrysididae) (Martynova 2020).



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## References

- Bonelli B (1967) Osservazioni biologiche sugli Imenotteri melliferi e predatori della Val di Fiemme. XXVI. Bollettino dell'Istituto di Entomologia della Università degli Studi di Bologna 28: 305–317. [+ pls I–III]
- Gonzalez VH, Gustafson GT, Engel MS (2019) Morphological phylogeny of Megachilini and the evolution of leaf-cutter behavior in bees (Hymenoptera: Megachilidae). Journal of Melittology 85: 1–123. <https://doi.org/10.17161/jom.v0i85.11541>
- Ivanov SP, Fateryga AV (2018) Nesting biology of the bee *Hoplitis princeps* (Morawitz) (Hymenoptera, Megachilidae) in Crimea. Entomological Review 98(8): 995–1005. <https://doi.org/10.1134/S0013873818080067>
- Ivanov SP, Filatov MA (2008) Nest cells construction of wild bees *Megachile albisecta*, *Hoplitis mocsaryi* and *Osmia tergestensis* (Hymenoptera: Apoidea: Megachilidae). Kharkov Entomological Society Gazette 15(1–2): 109–116. [In Russian]
- Ivanov SP, Zhidkov VYu (2010) Variety of the forms and sizes of leaf-cuts used by leafcutter-bees (Hymenoptera: Megachilidae, *Megachile* Latreille) when building their nests and theirs functional role. Proceedings of the Russian Entomological Society 81(2): 103–111. [In Russian]
- Koller F, Hamann HHF (1950) Nestbau von *Osmia mitis* Nyl. (= *montivaga* Mor.) Hymenopt. (Apidae). Naturkundliche Mitteilungen aus Oberösterreich 1: 16–17. [+ pl. II]
- Maneval H (1925) Nidification de l'*Osmia mitis* Nyl. [Hym. Apidae]. Bulletin de la Société Entomologique de France 30(12): 199–200. [+ pl. 2] <https://doi.org/10.3406/bsef.1925.27526>
- Marikovskaja TP (1968) New data on the biology of some species of colonial bees (Hymenoptera, Megachilidae) from South-East Kazakhstan. Entomologicheskoe Obozrenie 47(4): 796–805. [In Russian]
- Martynova KV (2020) Cocoons of cuckoo wasps (Hymenoptera: Chrysididae): first overview of morphology reveals unexpected traces of taxonomy. Zoologischer Anzeiger 285: 122–138. <https://doi.org/10.1016/j.jcz.2020.02.002>
- Michener CD (2007) The bees of the world (2<sup>nd</sup> edn). Johns Hopkins University Press, Baltimore, [xvi +] 953 pp. [+ 20 pls]
- Morawitz F (1871) Neue suedeuropaeische Bienen. Horae Societatis Entomologicae Rossicae 8(3): 201–231.
- Müller A (2015) Nest architecture and pollen hosts of the boreoalpine osmiine bee species *Hoplitis (Alcidamea) tuberculata* (Hymenoptera, Megachilidae). Journal of Hymenoptera Research 47: 53–64. <https://doi.org/10.3897/JHR.47.7278>



- Müller A (2020) Palaearctic *Osmia* bees of the subgenera *Hemiosmia*, *Tergosmia* and *Erythrosmia* (Megachilidae, Osmiini): biology, taxonomy and key to species. *Zootaxa* 4778(2): 201–236. <https://doi.org/10.11646/zootaxa.4778.2.1>
- Müller A (2023) Palaearctic Osmiine Bees, ETH Zürich. <http://blogs.ethz.ch/osmiini> [accessed 3 September 2023]
- Müller A, Krebs A, Amiet F (1997) Bienen. Mitteleuropäische Gattungen, Lebensweise, Beobachtung. Naturbuch Verlag, Augsburg, 384 pp.
- Nugroho H, Ubaidillah R, Kojima J (2016) Taxonomy of the Indo-Malayan presocial potter wasp genus *Calligaster* de Saussure (Hymenoptera, Vespidae, Eumeninae). *Journal of Hymenoptera Research* 48: 19–32. <https://doi.org/10.3897/JHR.48.7045>
- Praz CJ, Müller A, Danforth BN, Griswold TL, Widmer A, Dorn S (2008) Phylogeny and biogeography of bees of the tribe Osmiini (Hymenoptera: Megachilidae). *Molecular Phylogenetics and Evolution* 49(1): 185–197. <https://doi.org/10.1016/j.ympev.2008.07.005>
- Rozen Jr JG, Özbek H, Ascher JS, Sedivy C, Praz CJ, Monfared A, Müller A (2010) Nests, petal usage, floral preferences, and immatures of *Osmia* (*Ozbekosmia*) *avosetta* (Megachilidae: Megachilinae: Osmiini), including biological comparisons with other osmiine bees. *American Museum Novitates* 3680: 1–22. <https://doi.org/10.1206/701.1>
- Rozen Jr JG, Praz CJ (2016) Mature larvae and nesting biologies of bees currently assigned to the Osmiini (Apoidea: Megachilidae). *American Museum Novitates* 3864: 1–46. <https://doi.org/10.1206/3864.1>
- Rust RW (1980) Nesting biology of *Hoplitis biscutellae* (Cockerell) (Hymenoptera: Megachilidae). *Entomological News* 91(4): 105–109.
- Sedivy C, Dorn S, Müller A (2012) Molecular phylogeny of the bee genus *Hoplitis* (Megachilidae: Osmiini) – how does nesting biology affect biogeography? *Zoological Journal of the Linnean Society* 167(1): 28–42. <https://doi.org/10.1111/j.1096-3642.2012.00876.x>
- Seregin AP (2004) *Allium nathaliae* (Alliaceae), a new species from the Crimea (Ukraine, Europe), and taxonomic notes on the related species *A. erubescens* C. Koch. *Wulfenia* 11: 15–28.
- Ungricht S, Müller A, Dorn S (2008) A taxonomic catalogue of the Palaearctic bees of the tribe Osmiini (Hymenoptera: Apoidea: Megachilidae). *Zootaxa* 1865: 1–253. <https://doi.org/10.11646/zootaxa.1865.1.1>
- Westrich P (1989) Die Wildbienen Baden-Württembergs. Ulmer, Stuttgart, 972 pp.